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Tuning the developing brain to emotional body expressions

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Research Highlights

- ERPs were measured in response to emotional body expressions in infants using point-light displays
- 8-month-old infants, but not 4-month-old infants, discriminated between the orientation (upright, inverted) and the emotion (fearful, happy) of bodies in motion
- neural evidence for the developmental emergence of emotion perception from body cues

Abstract

Reading others' emotional body expressions is an essential social skill. Adults readily recognize emotions from body movements. However, it is unclear when in development infants become sensitive to bodily expressed emotions. We examined event-related brain potentials (ERPs) in 4- and 8-month-old infants in response to point-light displays (PLDs) of happy and fearful body expressions presented in two orientations (upright and inverted). The ERP results revealed that 8-month-olds but not 4-month-olds respond sensitively to the orientation and the emotion of the dynamic expressions. Specifically, 8-month-olds showed (i) an early (200-400 ms) orientation-sensitive positivity over frontal and central electrodes, and (ii) a late (700-1100 ms) emotion-sensitive positivity over temporal and parietal electrodes in the right hemisphere. These findings suggest that orientation-sensitive and emotion-sensitive brain processes, distinct in timing and topography, develop between 4 and 8 months of age.

Introduction

Reading others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Frijda & Mesquita, 1994; Frith, 2009; Izard, 1977, 2007). Emotional communication is inherently multidimensional and multisensory in nature as emotional information can be gleaned from various sources such as the face, the voice and the body posture and motion of a person (Heberlein & Atkinson, 2009). The bulk of research investigating emotion expression perception has focused on facial and vocal expressions (Belin, Campanella, & Ethofer, 2012). Much less work has been dedicated to understanding the perception of emotional body expressions, even though body expressions may be the most evolutionarily preserved and immediate means of conveying emotional information (de Gelder, 2006). The work on emotional body expressions has revealed that adults are readily able to detect and recognize various emotions from body expressions (Atkinson, 2013; de Gelder, 2009). This ability to recognize emotions from body expressions relies on specific brain processes localized principally in the right hemisphere, including superior temporal, somatosensory and premotor cortices (Atkinson, 2013; de Gelder, 2006; Grèzes, Pichon, & de Gelder, 2007; Heberlein, Adolphs, Tranel, & Damasio, 2004; Heberlein & Saxe, 2005).

Already during the first year of life infants become sensitive to various facial and vocal expressions (Grossmann, 2012). In particular, there is behavioral and neural evidence to suggest that infants begin to discriminate between positive and negative emotional expressions during the first year of life (Vaish, Grossmann, & Woodward, 2008). For example, 7-month-old infants but not 5-month-old infants showed longer looking times to fearful faces when compared to happy faces and differences in their event-related brain potentials (ERPs) during the processing of these facial expressions, indicating that infants' ability to discriminate between emotions emerges

during the first year of life (Nelson & de Haan, 1996; Peltola, Leppänen, Mäki, & Hietanen, 2009). Specifically, a series of ERP components discriminate between fearful and happy expressions (early-latency: Positivity before [Pb], mid-latency: Negative component [Nc], and late-latency Positive component [Pc]) (Nelson & de Haan, 1996); these components are thought to be associated with attentional/novelty (early Pb and mid-latency Nc) and recognition memory (late-latency Pc) processes engaged by infants during visual experiments (see Webb, Long, & Nelson, 2005). Critically, ERP differences similar to those that discriminate between facial expressions have been described in 7-month-olds when angry voices were compared to happy and neutral voices (Grossmann, Oberecker, Koch, & Friederici, 2010; Grossmann, Striano, & Friederici, 2005), suggesting that the sensitivity to emotional information across face and voice emerges during the first year of life. Indeed, there is ERP evidence showing that 7-month-old infants can integrate emotional information across face and voice (Grossmann, Striano, & Friederici, 2006). Specifically, in this study, 7-month-olds showed an enhanced late-latency Pc, when emotional information matched across face and voice, indexing the recognition of common affect across modalities, while mismatching emotional information resulted in a greater mid-latency Nc, indexing greater allocation of attention to novelty. Despite the progress that has been made in understanding the ontogeny of emotion perception from face and voice, how the ability to perceive and respond to others' emotional body expressions develops during infancy is only poorly understood.

This is an important question because from very early in development infants have been shown to be sensitive to biological motion, serving as a foundation for detecting and interpreting body movements. Behavioral research using point-light displays (PLDs) (Johansson, 1973) suggests that, from birth, human infants prefer to look at biological motion (e.g. walking hen)

over non-biological motion (e.g. randomly drifting dots), and they also show a preference for upright over inverted biological movement (for similar findings with 3-month-old infants using point-light walkers see Bertenthal, 1993; Simion, Regolin, & Bulf, 2008). Infants have also been shown to detect distortions of body configuration at 3 months of age (Gliga & Dehaene-Lambertz, 2005) and perceive human point-light displays as solid forms at 5 months of age (Moore, Goodwin, George, Axelsson, & Braddick, 2007), suggesting that they are sensitive to form and form-from-motion information related to the configuration of body parts. These findings suggest that human infants possess an early developing system that allows for the detection of biological motion and human bodies.

This early perceptual sensitivity to biological motion can also be traced at the neural level. In one study, upright compared to inverted human point-light motion elicited a greater right posterior positivity (P290) at parietal sites in 8-month-old infants' ERPs (Reid, Hoehl, & Striano, 2006). In another ERP study, 8-month-olds showed greater (more negative) amplitude ERPs at right parietal sites 200 to 300 ms post stimulus onset to upright motion in PLDs when compared to scrambled point-light motion (Hirai & Hiraki, 2005). Despite the inconsistencies concerning the direction of the modulation of the ERP component across these studies, these findings suggest that 8-month-olds' neural systems are able to detect human biological motion and this likely relies on posterior regions in the right hemisphere. In 5-month-old infants, the ERP effect discriminating between upright and scrambled motion was not lateralized to the right hemisphere as in 8-month-olds but observed at posterior electrode sites over both hemispheres (Marshall & Shipley, 2009). This suggests that the right hemisphere dominance in dealing with biological motion cues emerges only after 5 months of age.

Although much work has been concerned with infants' emerging abilities to make sense of bodies in motion, so far only one published study has addressed the development of the ability to sensitively respond to emotional information carried in body motion. Zieber and colleagues (2014) examined infants' ability to discriminate between emotional body expressions in a series of behavioral experiments with 6.5-month-old infants (using video full-light body expressions taken from Atkinson, Dittrich, Gemmell, & Young, 2004; Atkinson, Tunstall, & Dittrich, 2007). In this study, 6.5-month-olds showed a visual preference for happy over neutral body expressions and were shown to look longer at body-voice pairings that conveyed congruent emotional information (happiness or anger) than incongruent emotional information. Critically, these effects were specific to body expressions presented in an upright orientation, since infants did not show any difference in their looking responses when the body expression was presented upside-down (Zieber, Kangas, Hock, & Bhatt, 2014). While these findings provide first insights into infants' perceptual ability to discriminate between emotional body expressions, there are a number of vital remaining questions that are addressed in the current study. In particular, it is not known: (a) what neural processes underpin the behaviorally expressed sensitivity, (b) whether the brain responses elicited by positive and negative bodily expressed emotions are similar to those elicited by facial and vocal expressions, and (c), at what age this (neural) sensitivity to bodily expressed emotions develops.

Therefore, the aim of our study was to investigate the developmental emergence of infants' neural sensitivity to emotional body expressions. We examined when the infant brain becomes tuned to emotional body expressions by presenting 4- and 8-month-olds with upright and inverted happy and fearful dynamic body expressions using PLDs. We used PLD stimuli because they provide very little static information and no information regarding the facial expression but

contain the essential motion cues that allow adult observers to recognize emotions from body motion (Atkinson et al., 2004; Atkinson et al. 2007). We had three main predictions with respect to infants' developing ability to discriminate emotional body expressions. First, based on prior work using facial and vocal expressions (Grossmann et al., 2005; Nelson & de Haan, 1996; Peltola et al., 2009) we predicted that 8-month-olds, but not 4-month-olds, would be able to discriminate between emotional expressions conveyed through body movement. Second, based on prior work that has shown that body expression perception in adults is impaired (but not abolished) by stimulus inversion (Atkinson et al., 2007; Stekelenburg & de Gelder, 2004), we predicted that infants' discrimination between emotions would mainly be evident in the upright condition but not, or at least not as clearly, in the inverted condition (see Zieber et al., 2014 for behavioral evidence showing that infants' detect emotional information better in upright orientation). Third, given previous findings of right-hemisphere lateralization of emotional body-expression processing in adults (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), we predicted that the brain responses indicating the ability to discriminate between emotional body expressions in infants will be observed mostly or only over the right hemisphere. In addition, with respect to infants' sensitivity to the orientation (upright or inverted) of body expression, we predicted a main effect of stimulus orientation similar in topography and timing to Reid and colleagues' (2006) ERP findings with 8-month-olds using upright and inverted walking and kicking movements. Given that the current study was the first to examine orientation effects using ERP measures in infants younger than 8 months, we did not have any specific predictions concerning development of the ERP responses to orientation of body movements. However, prior behavioral work suggests that infants younger than 8 months of age are sensitive to stimulus inversion as indexed by a looking preference for upright movement

(Berthenthal, 1996; Simion et al., 2008).

Materials and Methods

Participants. The final sample consisted of 20 four-month-old infants aged between 123 and 137 days (10 females, *Median age* = 129 days, *Range* = 14 days) and 20 eight-month-old infants between 230 and 259 days (9 females, *Median age* = 251, *Range* = 29 days). An additional 15 four-month old infants and 20 eight-month-old infants were tested but were excluded from the final sample due to fussiness ($n = 5$) or too many artifacts ($n = 30$). The infants were born full-term (between 37 and 41 weeks) and had a normal birth weight (> 2500 g). All parents gave informed consent prior to the study. Ethical approval was obtained from the ethics committee of the University of Leipzig. All parents provided written informed consent prior to the study and were paid for their children's participation. The children were given a toy after the session.

Stimuli. The stimulus material consisted of 2-second clips of point-light body movements displaying eight different fearful and eight different happy expressions (from Atkinson, Vuong, & Smithson, 2012), which were presented upright and inverted (see Figure 1). Stimulus inversion was achieved by creating vertical mirror duplicates of the upright stimuli. Stimulus motion was equated across the two emotion categories by selecting 8 expressions from the original set of 10 for each emotion, such that the differences in the means of 3 similar measures of stimulus motion were as small as possible. Stimulus motion was calculated as the sum of the distance, in pixels, traveled by the dots in each display (a) from one frame to the next across the length of the movie clip (fearful $M = 1212.50$, happy $M = 1329.00$), (b) across every two frames (fearful $M = 1157.75$, happy $M = 1296.88$) and (c) every three frames (fearful $M = 1140.25$, happy $M = 1237.13$). Pairwise comparisons revealed no differences between fearful and happy

displays for any of the 3 measures (all $t_s < 0.9$, all $p_s \geq .4$).

insert Figure 1 about here

Procedure. The infants were seated on their parent's lap in a dimly lit, sound-attenuated and electrically shielded room during testing. The stimuli were presented in the center of the screen on a black background, using a 70-Hz, 17-inch computer screen at a distance of 70 cm. Each trial began with an alerting sound and a fixation cross (1000 ms), in order to attract the infants' attention to the screen, followed by a black screen (400 ms) and then a point-light body expression movie clip (2000 ms). During the inter-trial interval infants were presented with an abstract screensaver for the purpose of keeping infants' attention. The inter-trial interval lasted at least 1000 ms and varied depending on the infants' attentiveness, as stimulus presentation was controlled by an experimenter in such a way that stimuli were only presented when infants were looking at the screen. The stimuli were presented in a randomized order with the exception that no two stimuli with the same emotion and orientation combination were presented consecutively. In addition, the sessions were video-recorded to off-line code for infants' attention to the stimulus. The EEG session ended when the infant became fussy, or inattentive.

ERP analysis. The EEG was recorded from 27 Ag/AgCl electrodes attached to an elastic cap (EasyCap GmbH, Germany) using the 10-20 system of electrode placement. The data were online referenced to the CZ electrode and offline re-referenced to the algebraic mean of the left and right mastoid electrode. The horizontal electrooculogram (EOG) was recorded from two electrodes (F9, F10) that are part of the cap located at the outer canthi of both eyes. The vertical

EOG was recorded from an electrode on the supraorbital ridge (Fp2) that is part of the cap and an additional single electrode on the infraorbital ridge of the right eye. The EEG was amplified using a Porti-32/M-REFA amplifier (Twente Medical Systems International) and digitized at a rate of 500 Hz. Electrode impedances were kept between 5 and 20 k Ω . Data processing for ERP analysis was performed using an in-house software package EEP, commercially available under the name EEProbeTM (Advanced Neuro Technology, Enschede). The raw EEG data were bandpass filtered between 0.3 and 20 Hz. The recordings were segmented into epochs time-locked to the start of the video clip. The video clips were cut in such a way that the video clip onset coincided with the movement onset of the PLD. The epochs were baseline corrected by subtracting the average voltage in the 200 ms baseline period (prior to video or picture onset) from each post-stimulus data point. The baseline period contained a 200 ms black screen. Data epochs were rejected off-line whenever the standard deviation within a gliding window of 200 ms exceeded 80 μ V in any of the two bipolar EOG channels and 60 μ V at EEG electrodes. EEG data were also visually inspected offline for artifacts. At each electrode, artifact-free epochs were averaged separately for fearful upright, happy upright, fearful inverted and happy inverted body expressions to compute the ERPs. The criterion for the minimum number of trials for inclusion in the final ERP average was 7 artifact free trials per condition. For the 4-month-olds the mean number of trials seen per condition was 17.81. The mean number of trials included in the ERP average was 11.10 for the fearful upright condition, 11.40 for happy upright, 10.55 for fearful inverted and 10.30 for the happy inverted condition. The minimum number of trials was 7 and the maximum number of trials was 19. For the 8-month-olds the mean number of trials seen per condition was 19.98. The mean number of trials included in the ERP average was 11.45 for the fearful upright condition, 11.80 for the happy upright condition, 10.75 for fearful inverted and

12.10 for the happy inverted condition. The minimum number of trials was 7 and the maximum number of trials was 20. While the mean number of trials included in the final analysis might appear lower than in previous studies, note that we used dynamic video stimuli that were substantially longer in duration than in previous studies. Furthermore, we applied a strict criterion for inclusion in the analysis, which required the entire trial epoch (2200 ms) to be artifact free (for a similar design using video material and similar analysis criteria, see Grossmann, Missana, Friederici, & Ghazanfar, 2012). Decisions pertaining to the statistical analyses were informed by visual inspection of the ERP waveforms and by prior work focusing on infant facial expression processing (Nelson & de Haan, 1996; Peltola et al., 2009). Specifically, based on this information, three consecutive time-windows were selected to investigate effects of the experimental manipulations on the three ERP components (Pb: 200-400 ms, [early-latency component], Nc: 400-700ms, [mid-latency component], Pc: 700-1100ms [late-latency component]). To account for the longer latencies (approximately 100 ms longer) for the ERP components in the group of 4-month-old infants, the time windows for the ERP analyses were shifted by 100 ms for all three ERP components (Pb, Nc, and Pc). These components have been commonly studied in visual experiments in infants (Webb et al., 2005) and have been shown to be modulated by facial emotional information (happy versus fear) in prior work (Nelson & de Haan, 1996). The selection of regions of interest was informed by visual inspection of the ERP waveforms and prior work using point-light displays (Hirai & Hiraki, 2005; Reid et al., 2006) and happy and fearful emotional facial expressions (Nelson & de Haan, 1996; Peltola et al., 2009). Specifically, based on this information, ERP effects were examined for two regions of interest: (1) an anterior fronto-central region of interest including frontal and central electrodes (F3, F4, C3, C4) for analyzing the Pb, Nc, and Pc, and (2) a more posterior temporo-

parietal region of interest including temporal and parietal electrodes (T3, T4, P3, P4) for analyzing the Pc. This latter region of interest was chosen because in prior work effects on the Pc were reported over both fronto-central and temporo-parietal regions (de Haan & Nelson, 1997; Grossmann et al., 2006). In keeping with prior work (Leppänen et al., 2007), main statistical analyses were carried out separately for the two age groups. Mean amplitude ERP effects for these regions and time windows were assessed in repeated measures ANOVAs with the within-subject factors emotion (happy versus fear), orientation (upright versus inverted), and hemisphere (left versus right). Main statistical analyses were carried out separately for the two age groups because (a) it has been recommended not to combine ERPs for infants more than 1- to 2-months apart in age (DeBoer, Scott, & Nelson, 2005), and (b) prior work suggests that Pb, Nc and Pc undergo developmental change during this period of infancy (Webb et al., 2005) (see Figure 2). In addition, in order to examine potential age differences in our study the factor age was added as a between-subjects factor in supplementary analyses.

Results

Pb (200-400 ms). Our analysis for the Pb revealed a significant main effect of orientation at the anterior region of interest (frontal and central electrodes) in 8-month-old infants, $F(1, 19) = 4.788$, $p = 0.041$, $\eta^2 = 0.201$. In particular, inverted body expressions elicited a larger (more positive) Pb ($M = 7.588 \mu V$, $SE = 1.651$) than upright body expressions ($M = 4.083 \mu V$, $SE = 1.6$). No other main effects or interactions reached significance. No effects on the Pb were observed in the group of 4-month-old infants (all F s < 1.301). Additional analysis comparing Pb responses across ages revealed no significant interactions with age (all F s < 2.95).

Nc (400-700 ms). Our analysis for the Nc revealed that infants did not show any significant effects at either age or region. However, given that there was a significant main effect of the factor stimulus orientation in the group of 8-month-old infants during the early time window (Pb: 200-400 ms), we carried out a further analysis that assessed the effects of emotion separately for the two stimulus orientations (upright and inverted) at fronto-central electrodes. No significant effects or interactions reached significance (all $F_s < 1.421$). No effects on the Nc were observed in the group of 4-month-old infants (all $F_s < 1.404$). Additional analysis comparing Nc responses across ages revealed no significant interaction with age (all $F_s < 1.155$).

Pc (700-1100 ms). For the group of the 8-month-old infants the analysis revealed a significant effect for orientation at anterior electrodes, $F(1, 19) = 6.495$, $p = 0.020$, $\eta^2 = 0.255$. Inverted body expressions elicited a more positive amplitude ($M = 1.223 \mu V$, $SE = 1.171$) than upright body expressions ($M = -1.465 \mu V$, $SE = 1.264$). No other significant differences were found (all $F_s < 1.726$). No significant effects were observed in the group of 4-month-old infants (all $F_s < 3.689$; this F -value resulted from a marginally significant main effect of the factor hemisphere, $F(1, 19) = 3.689$, $p = 0.07$). Additional analysis comparing Pc responses across ages revealed no significant interaction with age (all $F_s < 3.344$; this F -value resulted from a marginally significant interaction between the factors orientation and age, $F(1, 19) = 3.344$, $p = 0.075$).

Our analysis for the Pc at the posterior region of interest (temporal and parietal electrodes) revealed a significant three-way interaction between the factors emotion, hemisphere and age, $F(1, 38) = 4.746$, $p = 0.036$, partial $\eta^2 = 0.111$. In further analyses a significant interaction between emotion and hemisphere for the posterior region of interest in 8-month-old infants was found, $F(1, 19) = 8.05$, $p = 0.011$, $\eta^2 = .298$. For this posterior region mean amplitude during this time

window differed between emotions only in the right hemisphere, $F(1, 19) = 5.524$, $p = 0.03$, $\eta^2 = .225$ (where happy body expressions elicited a larger (more positive) Pc [$M = 1.349 \mu\text{V}$, $SE = 1.138$] than fearful body expressions [$M = -0.688 \mu\text{V}$, $SE = 1.1$]), but not in the left hemisphere. More specifically, this discrimination between emotions in the right hemisphere at posterior electrodes appeared to be driven by the upright condition, in which happy body expressions elicited a more positive Pc [$M = 1.821 \mu\text{V}$, $SE = 1.415$] than fearful body expressions [$M = -2.076 \mu\text{V}$, $SE = 1.341$], $t(19) = 2.551$, $p = 0.02$, whereas no such differences were observed in the inverted condition, $t(19) = 0.141$, $p = 0.889$ (happy body expressions [$M = 0.877 \mu\text{V}$, $SE = 1.393$], fearful body expressions [$M = -0.7 \mu\text{V}$, $SE = 1.436$]). We justified these separate analyses of the effects of emotions for the two stimulus orientations (upright and inverted) on the basis of the finding of a main effect of stimulus orientation during an early time window (Pb: 200-400 ms). No effects on the Pc were observed in the group of 4-month-old infants (all F s < 1.402).

 insert Figure 2 about here

Discussion

In this study, we examined ERPs in 4- and 8-month-old infants in response to dynamic displays of happy and fearful body expressions presented in two orientations (upright and inverted). Our ERP results revealed that 8-month-olds but not 4-month-olds respond sensitively to the orientation and the emotion of the dynamic body expressions. Specifically, 8-month-olds showed (i) an early (200-400 ms) orientation-sensitive Pb at frontal and central electrodes, and

(ii) a late (700-1100 ms) emotion-sensitive Pc at temporal and parietal electrodes over the right hemisphere. These findings demonstrate that orientation-sensitive and emotion-sensitive brain processes, that are distinct in timing and topography, develop between 4 and 8 months of age. The ERP data therefore provide evidence that an important developmental transition in the neural processing of body expressions occurs between 4 and 8 months of age.

Our ERP results show that it is not until around the age of 8 months are infants' brains able to distinguish between upright and inverted body motion from PLDs. The current study was the first to examine orientation effects using ERP measures in infants younger than 8 months of age, and the ERP responses measured indicate that younger infants fail to distinguish between upright and inverted body movements. This might be seen as discrepant to prior behavioral work suggesting that younger infants (newborns and 3-month-olds) are sensitive to stimulus inversion as indexed by a looking preference for upright movement (Bertenthal, 1996; Simion et al., 2008). However, it should be noted that a similar dissociation between neural and behavioral measures is evident when examining the work investigating face inversion effects (de Haan, Pascalis, & Johnson, 2002; Farroni et al., 2005). This may have to do with the fact that in looking time studies stimuli are presented for much longer durations allowing for greater exploration by the infants, whereas in ERP studies stimuli are presented for much shorter durations required for the rapid detection of the relevant information. In any case, our data show an orientation-sensitive ERP response in 8-month-old infants during an early time window (between 200 and 400 ms). The timing of this ERP effect is in line with prior ERP work with 8-month-old infants using upright and inverted kicking and walking motion (Reid et al., 2006), suggesting that orientation of body motion is detected during early processing stages. However, while in the current study the orientation-sensitive ERP response (Pb) was found to be greater in amplitude to inverted

body motion and observed at frontal and central electrodes, prior work found that *upright* body motion elicited larger positivity at posterior (parietal) electrodes, suggesting that topography and direction of modulation of the orientation-sensitive ERP response differ across studies. This difference might be explained by the fact that across these studies the PLD stimuli varied with respect to the kind of movement displayed. Namely, Reid and colleagues (2006) used walking and kicking movements that provide cues regarding the direction of biological motion in the horizontal plane to the infant, which may result in evoked activity in brain regions sensitive to such directional information (de Lussanet et al., 2008; Oram & Perrett, 1994; Vangeneugden et al., 2011). It is important to emphasize that, in Reid and colleagues (2006) study, the directional cues were in principal also available in the inverted condition, however, the coding of the direction of body movement may require for the body motion to be presented in the upright orientation (Gurnsey, Roddy, & Troje, 2010; Troje & Westhoff, 2006).

In the current study, no uniform direction of body movement was evident across the stimulus set or in many of the individual stimuli, suggesting that infants' discrimination of upright and inverted body motion did not involve such directional cues but may have relied on more general brain processes detecting and discriminating familiar from unfamiliar visual events. Indeed, the current data show that the orientation-sensitive responding occurred for the Pb, which is an infant ERP component that has been found to be sensitive to the familiarity of a visual stimulus (Webb et al., 2005). Even though much less is known about the Pb than the Nc, prior work suggests that the response properties of the Pb are very similar to the Nc and may thus also reflect attentional resource allocation related to stimulus familiarity, whereby a smaller Pb is thought to reflect greater allocation of attention to a visual stimulus (Grossmann, 2012; Hoehl, Wiese, & Striano, 2008). This suggests that 8-month-old infants dedicated increased attentional

resources to processing upright body expressions. Increased attention to upright body expressions in 8-month-old infants may thus have an impact on later brain processes that follow the early orientation-sensitive ERP response.

Our analysis further revealed emotion-sensitive brain processing during a later time window (700-1100 ms). Critically, in line with our prediction based on prior work investigating facial and vocal emotion processing across infancy (Grossmann et al., 2010; Nelson & de Haan, 1996; Peltola et al., 2009), 8-month-old infants, but not 4-month-olds infants, distinguished between emotions. This supports the notion that brain processes associated with emotion detection and discrimination undergo some general development during this period of life (see Leppänen & Nelson, 2009). The finding that the ERP effect reflecting sensitive responding to emotional body expressions emerges between 4 and 8 months of age might be explained by a number of factors. One possibility is that the observation and own experience of emotional states plays a critical role in the emergence of these discrimination processes. In particular, it has been argued that towards the end of the first year of life, the frequent and repeated exposure to happy emotions in self and others shapes infants' responses to emotional information and their ability to distinguish between positive and negative emotions (Vaish et al., 2008). Another possibility is that infants develop a better grasp of emotions expressed by others as the result of more wide-ranging improvements in their social cognitive abilities that have been reported to occur towards the end of the first year of life, especially in relation to the sharing and understanding of the attention and intentions of others (Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Regardless of the exact mechanisms that underlie the developmental change observed between 4 and 8 months, our findings support the notion of an early ontogenetic

emergence of the ability to respond sensitively to emotions displayed by others, thus providing a vital foundation for later emerging empathic and prosocial abilities in infancy.

More specifically, 8-month-olds showed an increased Pc in response to happy when compared to fearful body expressions. In prior work it has been shown that the Pc reflects neural processes associated with recognition memory. In particular, this work demonstrated that an increased Pc indexes the recognition of an item (Grossmann et al., 2006; Nelson, Thomas, de Haan, & Wewerka, 1998). Therefore, an increased Pc in response to happy body expressions as observed in the current data suggests that 8-month-old infants recognized the highly familiar (positive) expression and discriminated it from the less familiar (negative) expression. Furthermore, recognition reflected in the Pc might occur at the categorical level, as prior work has shown that a greater Pc is specifically evoked by new individual exemplars of a familiar visual category (Grossmann, Gliga, Johnson, & Mareschal, 2009). This appears likely given that infants in the current study were confronted with completely new and several different exemplars of happy body expressions. Importantly, this finding is in line with prior work showing a similar modulation of the Pc in response to happy when compared to fearful facial expressions (Nelson & de Haan, 1996), suggesting that recognizing positive emotional information is reflected in a neural signature common to face and body processing.

Contrary to prior work using facial expressions (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Nelson & de Haan, 1996), we did not observe an effect of emotion for any of the earlier ERP components (Pb and Nc). This discrepancy might be explained by differences in the type of stimulus material used across studies. Notably, the stimuli differed not only regarding whether they provided bodily expressed or facially expressed emotions but also with respect to whether static or dynamic emotion displays were used. Importantly, in recent work, using ERPs

we examined 8-month-old infants' processing of happy and fearful full-light static body expressions taken at the peak of the expression (Missana, Rajhans, Atkinson, & Grossmann, under review) and found earlier emotion effects (N290 and Nc) than in the current study when using PLDs. This suggests that the discrimination of emotions from bodily expressions occurs faster for static displays than for dynamic displays, which is likely to do with the fact that in the dynamic context the emotional expression unfolds over time, whereas in the static context the peak of the expression is presented immediately.

Confirming our predictions, our findings further revealed that infant brain response sensitive to emotional body expressions (Pc) was lateralized to the right hemisphere. This finding is in agreement with prior work on biological motion processing with 8-month-old infants (Hirai & Hiraki, 2005; Reid et al., 2006) and emotional body expression processing with adults (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005) that has also shown a lateralization of the brain responses to the right hemisphere. It should also be noted that this finding is in line with prior infant ERP research on the Pc, suggesting that this ERP component is lateralized to the right hemisphere and can be localized to the temporal cortex (Nelson, 1996; Reynolds & Richards, 2005). This furthers the notion that right hemispheric processes play an important role in the perception of emotions from body movement. While this finding is in overall agreement with prior work concerning body movement processing, no lateralization in the ERP responses sensitive to facial and vocal expressions of emotions was reported in previous studies with infants (Grossmann et al., 2005; Peltola et al., 2009). This suggests that body expression processing during infancy might rely more exclusively on brain processes localized in the right hemisphere than facial and vocal expression processing. However, more work possessing better brain activation localization properties than ERPs such as functional near-infrared spectroscopy

(fNIRS) with infants (for a review, see Lloyd-Fox, Blasi, & Elwell, 2010) is needed to obtain a clearer picture regarding the lateralization of infant brain responses.

With respect to the developmental change observed in the current ERP study one limitation should be discussed. Namely, in our additional analysis, we did not observe any interactions of the factor age (4 versus 8 months) with any of the ERP effects related to infants' discrimination of upright and inverted PLDs and happy and fearful PLDs. This indicates that, while our ERP data show that only at the age of 8 months, but not at 4 months, infants discriminate between the orientation and the emotion of a PLD, the ERP differences across age are not evident when directly assessed by including age as a between-subjects factor in our analyses. One possibility is that the age difference is not as strong as suggested by the results from the analyses carried out separately for the two ages, which might have to do with the fact that at least some of the 4-month-olds showed similar ERP responses to the 8-month-olds. In any case, it should be emphasized that the common way to assess development in infant perception research is by examining effects separately for different age groups as was done in the current study. Therefore, our analytical approach is in keeping with most prior work in this regard. Nonetheless, further work is needed to clarify the exact nature and time course of the identified developmental change.

This is the first study to use PLD body stimuli to display emotions to infants (previous behavioral work had relied on full-light displays of emotional expressions, Zieber et al., 2014). PLDs provide little static form information but contain the essential motion cues that allow adult observers to recognize emotions from body motion (Atkinson et al., 2004; Atkinson et al., 2007). Using PLDs we were able to show that 8-month-old infants can discriminate between emotional body expressions on the basis of motion cues. This finding critically extends prior work that has

investigated infants' perception of biological motion from PLDs (Bertenthal, 1993; Hirai & Hiraki, 2005; Reid et al., 2006) by showing that infants can detect not only biological and human motion more generally but also extract specific information concerning the emotional state of the biological agent. Moreover, we observed that inversion of the body motion disrupts the discrimination of emotions, as indicated by the finding that the Pc did only differ between emotions in the upright context but not in the inverted context (note that, in our analysis we did not obtain an interaction between the factors emotion and orientation, but that this finding relies on separate comparisons between emotions performed for the two stimulus orientation). This suggests that 8-month-old infants require upright body motion to successfully extract emotional information. This effect is in agreement with (a) what has been reported in adults who show impaired recognition of dynamic body expressions when presented upside down (Atkinson et al., 2007) and (b) what has been shown in infants using behavioral looking time methods (Zieber et al., 2014). The ERP differences between fearful and happy stimulus conditions are unlikely to be purely the result of differences in low-level motion properties between the two stimulus sets, however, for two reasons. First, we controlled for the amount of dot motion across the happy and fearful expressions. Second, the ERP differences between emotions were not evident for the inverted PLD stimuli, in which the available kinematic and dynamic information is identical to that available in the upright stimuli. Thus 8-month-olds are likely to be using higher-level motion cues, such as form-from-motion information or kinematics, to discriminate between the emotions.

Taken together, the findings presented in the current study have informed, at three levels, our understanding of how emotional body expressions are processed. First, at the developmental level, we have seen that over the course of the first year of life the human brain becomes tuned to emotional body expressions. The ontogenetic emergence of infants' ability to discriminate

emotional body expressions occurs at a time in development when facial and vocal emotion processing capacities undergo similar change. These findings thus provide evidence for accounts that conceive of emotion perception as a unified ability that develops in concert across various processing channels (face, voice and body). Second, at the perceptual level, we have shown that for emotion discrimination processes to occur the infant requires to see the body motion in an upright orientation. This is similar to what is known from adults (Atkinson et al., 2007) and it is also in line with work investigating the effects of inversion on the perception of faces in the first year of life (de Haan et al., 2002). The disruption of emotion discrimination by body inversion can be seen as evidence for the developmental emergence of configural processing of body motion. That is, rather than relying on individual features of the body that are also present in the inverted stimulus, 8-month-olds require to see the configuration of body features in order for the discrimination process to take place. Third, at the neural level, we have shown that emotion discrimination from body expressions elicits brain responses that are lateralized to the right hemisphere. In agreement with prior work (Grèzes et al., 2007; Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), this suggests that the right hemisphere begins to play an important role in emotional body expression processing from early in ontogeny. All in all, the current data has shed new light on the developmental, perceptual and neural processes that underpin emotional body expressions thereby critically extending and informing accounts of emotion perception.

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Figure Captions

Figure 1. This figure provides an example of the PLD stimuli. The figure shows two still frames taken at the maximum of the emotional expression.

Figure 2. This figure shows the event-related brain potentials (ERPs) time-locked to the stimulus onset in 4- and 8-month-old infants elicited by fearful upright (red solid line), fearful inverted (red dotted line), happy upright (blue solid line) and happy inverted (blue dotted line) point-light body expressions. The time windows during which significant differences were observed are marked in grey.

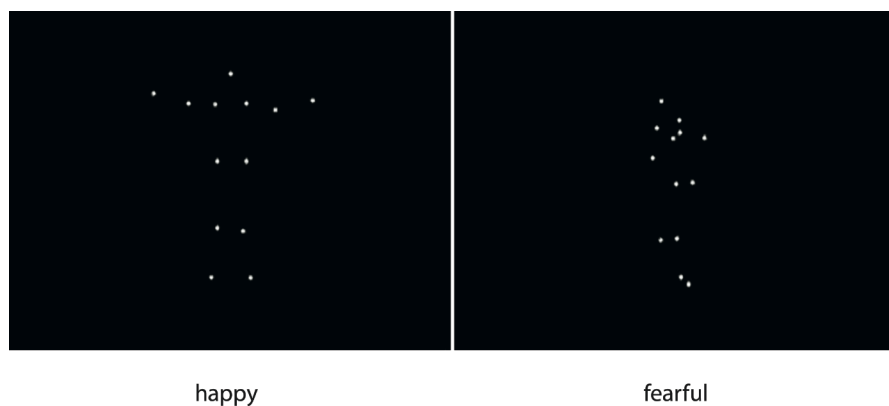


Figure 1.

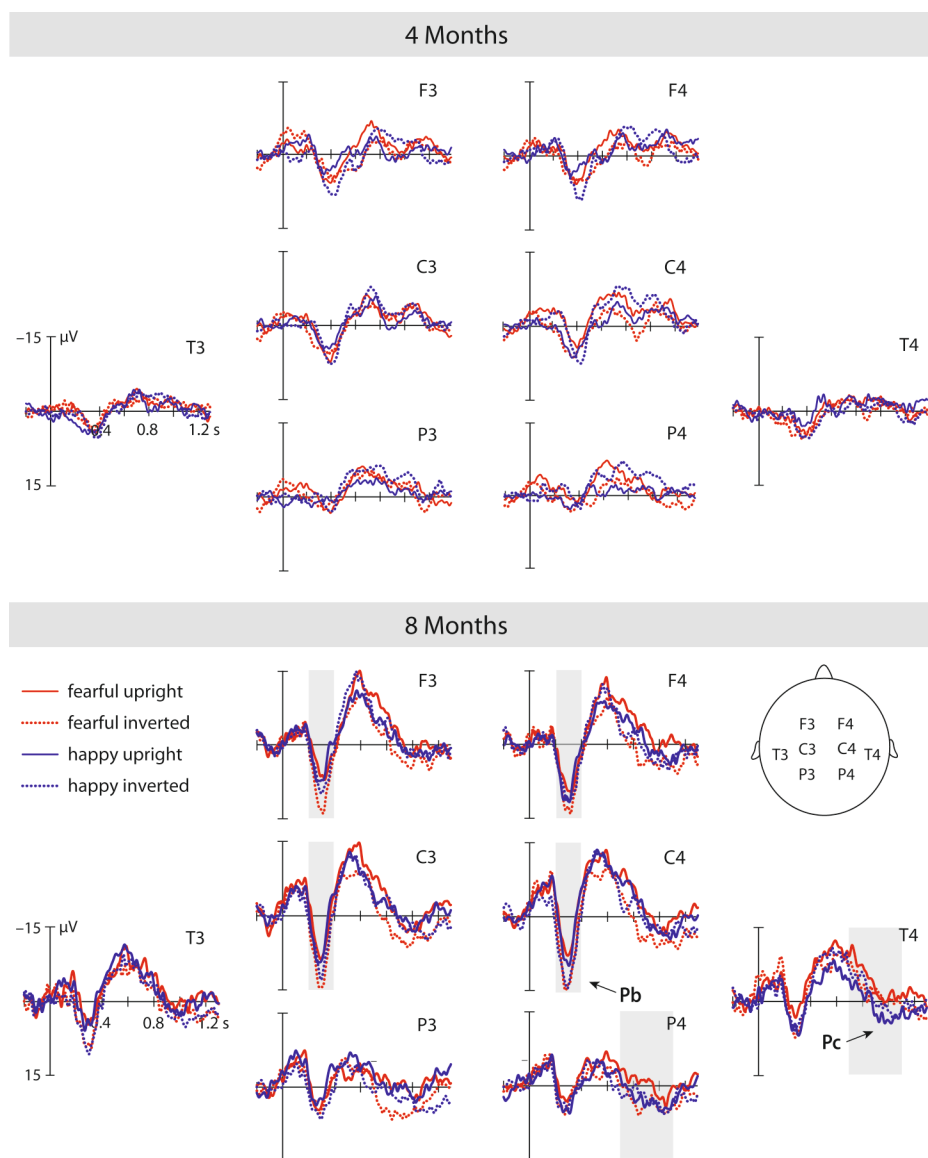


Figure 2.